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Physiology of interactions between mycorrhizae and rhizosphere microorganisms

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INTRODUCTION

From the soil microbiological point of view, any organic matter occurring in the soil is a potential nutrient resource for the microbial population which, thanks to its versatile enzymatic capability, is able to decompose all types of organic compounds but for a few recalcitrant ones. Generally, the growth of heterotrophic microbes in soil is, however, severely limited by shortage of energy-yielding substrates (GRAY and WILLIAMS, 1971). Hence the growing root systems of plants would be expected to be rapidly attacked by a multitude of microbes. The obvious restrictions of such attacks, i.e. the resistance of the root systems, and the special qualifications typical of those organisms which are able to function either as parasitic or mutualistic symbionts, constitute a challenge to the biologists.

The potential nutrient resource offered by the root systems consists of the root tissues themselves and of the organic matter leaked or secreted from the roots, as well as dead sloughed root cap and epidermal cells. As far back as in 1904, HILTNER introduced the term "rhizosphere" to mean the soil surrounding the roots where chemical and biological effects of the roots are exerted. STARKEY (1929 a,b) distinguished the following components of the rhizosphere effect: a) a diminution in the soil of certain mineral nutrients owing to root absorption; b) partial drying of the soil due to removal of water by the roots; c) increase in the carbonate due to carbon dioxide production in root and microbial respiration; d) growth of microorganisms which feed on disintegrating roots or their secretions. The origin, nature and nomenclature of the organic materials in the rhizosphere were summarized by ROVIRA, FOSTER and MARTIN (1979). Reviews of the literature on the mycorrhizosphere were published by a.o. BOWEN and THEODOROU (1973) and RAMBELLI (1973).

It is a general accepted view that the mycorrhizal fungi obtain their carbon- and energy-sources from the living roots whereas saprotrophic fungi utilize the organic substances in the litter and humus. How distinct is the difference between these two ecological groups of fungi? To what extent are the ectomycorrhizal fungi capable of decomposing complex organic matter like the cell wall components lignin, cellulose, hemicelluloses, pectin or even proteins and of producing the exoenzymes necessary for the decomposition of such substances? To what extent do these fungi contribute to the recycling of nutrients from the litter to the tree roots? Are there transitional facultative species, comprising strains which are able to live both as symbionts (biotrophs) and as litter-decomposers (saprotrophs)? What is the functional relation between the mycorrhizal fungi and the litter-decomposing saprotrophs? Questions like these seem to be relevant in a discussion of the physiology of interactions between mycorrhizae and rhizosphere microorganisms. A survey of the literature shows that the questions above are still a matter of dispute.

CARBON SOURCES OF ECTOMYCORRHIZAL FUNGI

Laboratory studies

The pioneering experimental work by MELIN (1925) indicated that the ectomycorrhizal fungi were in general able to utilize only glucose as a carbon source. MIKOLA (1948) studied the physiology and ecology of *Cenococcum graniforme*, especially as a mycorrhizal fungus of birch. Among several carbohydrates tested as carbon sources, only glucose, sucrose, maltose and mannitol were efficiently used by the fungus. However, growth on dextrin and starch was also noted. No indication of cellulose decomposition was observed.

Taking into consideration different aspects of the behaviour of *Cenococcum* in nature and in pure culture studies, MIKOLA concluded that "*Cenococcum* represents an intermediary form between mycorrhizal fungi proper and forest soil saprophytes".

NORKRANS (1950) found that mycorrhiza-forming *Tricholoma*-species, besides glucose, were able to utilize fructose and mannose and, to a lesser extent, maltose, sucrose and starch. When cultivated on cellulose in the presence of small amounts of "start" glucose, a weak cellulolytic effect was shown by a few species. NORKRANS concluded that "in many cases, the difference in cellulase-forming ability between litter-decomposers and mycorrhiza-formers is probably a quantitative rather than a qualitative one". According to her, the ectendomycorrhiza would be formed by certain fungal species when the plants for some reasons no longer form a surplus of soluble carbohydrates.

HACSKAYLO (1973) summarized most of the results obtained so far and discussed the experimental errors which might easily be overlooked in this type of research. It is clear that in many cases an enzyme must be induced to act on a special substrate and that this takes place only in the presence of another easily available carbon source (e.g. glucose, "start" glucose according to NORKRANS 1950). In addition the problem of how to sterilize a high molecular compound without breakdown may prove difficult to solve.

In summary, the monosaccharides glucose, fructose, mannose, the alcohol mannitol, and the disaccharides cellobiose, maltose, and trehalose seem to be utilized as carbon sources by most mycorrhizal species studied. Starch and dextrin can be utilized by some species.

The extent to which ectomycorrhizal fungi are capable of decomposing the cell wall components cellulose, pectin and lignin still remains a controversial question. Most authors agree that mycorrhizal fungi show a limited production - or no production at all - of the exoenzymes cellulase, pectinase, proteinase and laccase. However, the exceptions which have been documented are of great interest.

LINDEBERG (1948) found a strong laccase production in six *Lactarius* species, including *L. deliciosus*. GILTRAP (1982) extended the list of laccase-producing *Lactarius*-species by five other species. Indeed, it seems possible that laccase production is a character of this genus.

GILTRAP discusses the possibility that the genus *Lactarius* may be characterized as a genus of unspecialized, possibly facultative ectomycorrhizal fungi. However, he also draws attention to the facts that *Lactarius* species have not been observed to fruit in pure culture, nor do they have a broad host range, which again would not support the idea that they represent unspecialized ectomycorrhizal fungi.

TODD (1979) reported on experiments where the role of mycorrhizal fungi in organic matter decomposition was examined, utilizing axenic associations of Douglas fir with each of five common symbionts, e.g. *Cenococcum geophilum, Rhizopogon vinicolor, Laccaria laccata, Amanita pantherina* and *Suillus lakei*. Decomposition was assessed by measuring $^{14}CO_2$ respired by the mycorrhizal associations growing in peat-vermiculite, amended with various ^{14}C-labelled test substrates. Cellulose, hemicellulose, litter and a humic polymer were used as test substrates. All fungi tested were found to be capable of decomposing each substrate to a greater or lesser degree. Hemicellulose was decomposed more rapidly than cellulose, and cellulose more rapidly than litter. The humic polymer was most resistant.

NYLUND *et al.* (1981) showed that the ectomycorrhizal fungi *Pisolithus tinctorius* and *Piloderma croceum* regularly produced intracellular penetrations in senescent and dead cortical cells, while they were strictly intercellular in vital parts of the cortex of short roots. Senescent host cells occasionally produced papillae as a response to infection. The penetration was considered to be enzymatic, in spite of the fact that no cell wall lytic enzymes were demonstrated in these fungi.

GILTRAP and LEWIS (1982) studied the synthesis of pectin-degrading enzymes *in vitro* by *Suillus luteus*, which is an ectomycorrhizal fungus and *Hebeloma oculatum* which is a saprotrophic species of a genus which contains many mycorrhizal species. The synthesis of pectinolytic enzymes was repressed by glucose in both species. The authors suggest that catabolite repression functions as a control mechanism which prevents extensive intracellular fungal infection in ectomycorrhizae.

Recently, TROJANOWSKI, HAIDER and HÜTTERMANN (1984) studied five different species of known ectomycorrhizal fungi: *Cenococcum geophilum, Amanita muscaria, Tricholoma aurantium, Rhizopogon luteolus* and *Rhizopogon roseolus* for their ability to metabolize the major components of plant cell walls. All strains were able to decompose ^{14}C-labelled plant lignin, ^{14}C-lignocellulose, and ^{14}C-holocellulose, although at a rate much lower than what was found for the wood rotting fungi *Fomes annosus* and *Sporotrichum pulverulentum*. The authors conclude that "under the conditions in the top layer of forest soils where a mixed population of various litter-decomposing fungi is to be expected, mycorrhizal fungi may be able to contribute to the decomposition of litter-material".

Hence, evidence that has accumulated from *in vitro* experiments, seems to indicate that many ectomycorrhizal fungi are able to decompose different cell wall components, at least at slow rates and under special conditions.

In nature, however, the organic substances available to the fungi do not occur in a pure state. Water soluble compounds will be leached from the litter and the leachate will percolate through underlying strata under continuous transformation.

The effect of litter extracts on the growth of mycorrhizal and litter-decomposing basidiomycetes was studied by MELIN (1946), LINDEBERG (1944) and NORKRANS (1950). When added in small quantities, water extracts of various types of forest litter were found to stimulate the growth of mycorrhizal fungi in synthetic media, while higher concentrations of the extracts inhibited growth. On the contrary, the growth of litter-decomposing fungi was stimulated by litter extracts throughout the concentration range tested.

The stimulating effect was due partly to inorganic ions, mainly calcium and manganese, partly to unidentified organic factors. The inhibitory principles of aqueous extracts of aspen leaves were studied by OLSEN *et al.* (1971). Two inhibitors were identified as benzoic acid and catechol by gas chromatography and mass spectrometry. These substances had a strong inhibitory effect on the growth of different ectomycorrhizal species and a much weaker inhibitory effect on various litter-decomposing basidiomycetes.

Table 1. Effect on growth of fungi of catechol (Cat.), benzoic acid (BA), and extract of aspen leaf litter[a]

Addition	Mycorrhizal fungi		Litter decomposers	
	Boletus luteus	*Boletus variegatus*	*Marasmius perforans*	*Marasmius scorodonius*
None	100	100	100	100
Cat.	3	16	44	66
Cat. + BA	0.6	2	51	69
Extract	0.9	57	617	520
Extract + Cat.	1	7	200	456
Extract + Cat. + BA	0.9	2	295	457

[a] Concentration: Cat. and BA 0.5 mM, extract 20% v/v. Dry weight in percentage of control.

Source: Olsen *et al.* (1971).

The results indicate that water soluble aromatic substances play an important role in the microbial soil system. Due to their strong selective effect on the fungal flora, such substances will probably restrict the growth of mycorrhizal fungi in fresh litter. However, the litter-decomposing basidiomycetes generally produce extracellular phenol oxidases (LINDEBERG 1948) and probably cause an oxidative breakdown of aromatic compounds in the litter. This may imply that the aromatic inhibitors are successively eliminated so that the mycorrhizal fungi can penetrate further into the litter layers where they may compete for mineralized nutrients.

Field studies

In 1938 ROMELL introduced a simple method of trenching in order to study the effect on the vegetation and soil microflora obtained by isolating plots from the root systems of surrounding trees. In an old spruce forest, trenches were dug to a depth of 1 foot, and iron sheets, 1 foot high, were placed in the trenches before filling with mineral soil. The development of the vegetation and the fungal flora inside and outside the trenched plots was followed. The most striking results of the trenching were the following:

(1) complete disappearance of fruit bodies of mycorrhizal fungi within the plots;

(2) increased grass growth and darker shade of the green plants within the plots;

(3) delay of the autumn colour change of the plants within the plots.

The effects on the vegetation were similar to the effects obtained on parallel plots fertilized with nitrogen. ROMELL explains these results as a combination of a manuring effect caused by the killing-off of roots and mycorrhizae, and the effect of the ending of the competition for nutrients from the trees and their mycorrhizal fungi. The disappearance of fruit bodies of mycorrhizal fungi obviously supports the idea that these fungi depend on the carbon supply from the trees for fructification.

More recently, the trenching technique has been used by GADGIL and GADGIL (1971, 1975, 1978). They observed that, in stands of *Pinus radiata* in New Zealand, a dense mat of greyish-white mycelium, which binds together the semi-decomposed needles, is found under the freshly fallen undecomposed needles. They also found that this mycelium was basidiomycetous, bearing clamp connections.

In order to shed more light on the role of this mycelium, GADGIL and GADGIL made the following experiment: Four 1 x 1 m plots were marked out between the trees. In three of these plots, the bound~~e~~ary was cut to a depth of 30 cm so that all roots entering the plot down to this depth were severed. In this way, root activity within the plots was greatly reduced without impeding the movement of soil water or soil fauna. Because the severed roots would provide additional decomposable organic matter, as in the experiments of ROMELL, the following treatments were included:

1. After cutting the plot boundary, the litter on the plot was carefully removed onto a sheet of hessian cloth. The plot was dug to a depth of 30 cm and as many roots as possible were removed. The soil was smoothed over and the litter replaced.

2. The plot boundary was cut and the litter removed. Soil dug but roots not removed. Litter replaced.

3. Plot boundary cut. Litter removed and replaced. No digging.

4. Control plot. No cutting or digging but litter removed and replaced.

The plot boundaries were recut once a fortnight to ensure that no new roots penetrated the plots. After 12 months, all the litter from each plot was removed, dried and weighed. On this occasion it was observed that the mycelial mat which was conspicuous in the control plot had almost entirely disappeared from the cut plots. Obviously, the hyphae forming the mat were very closely associated with living roots.

Table 2. Effect of trenching on litter decomposition

Plots 1 x 1 m   Time 12 months

Treatment	Dry weight of litter (kg)
1. Roots cut and removed, dug	0.47
2. Roots cut, dug	0.35
3. Roots cut	0.66
4. Control	1.68

Source: GADGIL and GADGIL (1971)

It seems clear that the presence of living roots with mycorrhizae suppressed litter decomposition. The most probable reason for this suppression is the fact that the mycorrhizal fungi are highly efficient competitors for nutrients, e.g. nitrogen and phosphorus, due to their energy supply from the roots. Also, an antibiotic effect of certain mycorrhizal fungi cannot be excluded (KRYWOLAP *et al.*, 1964, MARX and DAVEY, 1969). As a consequence of the retardation of litter decomposition, the formation of mor is favoured.

Finally, according to HERRERA *et al.* (1978), tropical ecologists have long suspected that one of the nutrient-conserving mechanisms in the undisturbed rain forest of the Amazon basin is a direct recycling that involves the movement of nutrients from litter to the root mat which covers the soil surface. Such a nutrient-cycling pathway would reduce losses due to leaching. WENT and STARK (1968) hypothesized that mycorrhizal fungi are one of the pathways of transfer between litter and roots. These authors stress that, in the rain forest, the upper decomposing litter layer harbours a very dense network of hyphae and rhizomorphs, extending from decomposing leaves, branches and fruit pods to a very extensive network of feeder roots immediately below a layer of recently abscised leaves, only one to two leaves thick. All the roots appear to be mycorrhizal. WENT and STARK conclude that most of the litter on the floor of the rain forest is decomposed by fungi and that most of these fungi are mycorrhizal. Obviously, they assume that the mycorrhizal fungi in the rain forest are capable of decomposing the various high molecular components of litter. Experimental research on the physiology and biochemistry of the fungi in question would be of great interest.

AVAILABILITY OF HUMUS BOUND NITROGEN

A question of great interest in the discussion concerning the role of ectomycorrhizal fungi in the nutrient uptake of mycorrhizal roots is the possible capability of the fungi to utilize nitrogen bound in humic substances. In his classic work "Untersuchungen über die Bedeutung der Baummykorrhiza", MELIN (1925) expressed the opinion that different ectomycorrhizal fungi are probably able to utilize nitrogen in organic substances to different degrees. In an extensive investigation, LUNDEBERG (1970) cultivated several ectomycorrhizal and litter-decomposing species on "humus agar", containing ^{15}N-labelled humus, sterilized by gamma radiation. The experiments were performed in petri dishes, divided into two halves by means of diametric lists. Each petri dish received N-free glucose agar in the one half, and ^{15}N-labelled humus agar in the other one. Inocula with the fungi were placed across the separating lists so that the mycelia could grow out on both halves. The idea was that the glucose agar would correspond to the root tissue, the humus agar to the soil. An active transfer of ^{15}N from the humus agar half to the glucose agar half would indicate a mineralization of the nitrogen. Such a transport only occurred in experiments with saprophytic fungi. None of the mycorrhizal fungi tested gave a positive result.

INTERACTIONS BETWEEN ECTOMYCORRHIZAL FUNGI AND BACTERIA

Direct microscopy showed that the percentage cover of the root by microorganisms was only 10-20% (BOWEN and THEODOROU, 1973). Fungi and bacteria tend to grow along the junctions of epidermal cells where exudate and mucigel production is greatest (ROVIRA, 1956). BOWEN and THEODOROU (1979) studied interactions between various ectomycorrhizal fungi and different soil bacteria, namely pseudomonads and *Bacillus*-species, on laboratory media and in the rhizoplane of *Pinus radiata*. Depression of growth of the fungi by the bacteria in laboratory media varied with the composition of the media. Almost no correlation was found between the results on laboratory media and growth in the rhizoplane. The effect of the soil bacteria on the fungal colonization of the roots could be inhibiting, neutral, or stimulating. The reasons for depression could be competition for energy sources in some cases and antibiosis in others. One *Bacillus*-strain, isolated from *Rhizopogon luteolus* mycorrhiza, stimulated colonization by certain mycorrhizal fungi, indicating that mutualism at the microbial level could be of ecological significance. A direct positive effect of the bacterium on the fungi would be a possible explanation; or the effect could be the result of the bacterium increasing leakage of substrates from the root.

The specific properties of the mycorrhizosphere, including a reduced oxygen pressure, would indicate the possible occurrence of nitrogen-fixing bacteria within the rhizosphere. Some students of TRAPPE at Corvallis, LI and CASTELLANO (1984) found nitrogen-fixing *Klebsiella*- and *Pseudomonas*-like organisms in fruit bodies of different ectomycorrhizal fungi. Apparently, such bacteria may also be active within the sheath. The nitrogenase activity of the bacteria studied so far is, however, rather low.

CONCLUDING REMARKS

The classic view of the function of the ectomycorrhizal fungi states that these fungi can only utilize simple sugars (mono- and disaccharides) which they obtain from the tree roots. Owing to this comparatively rich supply of carbon- and energy sources and the wide distribution in the soil of mycelial strands and hyphae, the uptake of nutrients by the fungi is very efficient. On the other hand the mineralization of nutrients, bound in dead organic matter, is effected by the saprophytic microflora, including cellulose- and lignin-decomposing basidiomycetes.

As shown above, more recent results from different laboratories seem to indicate that there are, in fact, several exceptions in this picture. Different cell wall-degrading exoenzymes have been found in pure strains of single mycorrhizal species. The production of small amounts of cellulase in certain mycorrhizal *Tricholoma* species (NORKRANS, 1950) is a well known example. The occurrence of laccase in the genus *Lactarius* (LINDEBERG, 1948) as well as in *Cenococcum* (LUNDEBERG, 1970) has been confirmed by several workers. A capability in certain mycorrhizal strains to decompose and utilize pectin as a carbon source was observed by HOW (1950), RITTER (1964), PALMER and HACSKAYLO (1970), and GILTRAP and LEWIS (1982), whereas negative results with the same and closely related species were obtained by others (LYR, 1963; LUNDEBERG, 1970; LINDEBERG and LINDEBERG, 1977). In this connection, however, it is important to remember that different strains of one and the same species may show considerable quantitative differences with respect to the production of special enzymes.

LEWIS (1973) proposes an evolution of mycorrhizal fungi from saprotrophs, implying a repression of cell wall decomposing enzymes, finally leading to a genetic loss of the ability to produce such enzymes. According to this view, the occurrence of cellulase, pectinase, laccase and so on in certain mycorrhizal species should be regarded as a primitive character, indicating at least a possible facultative mode of life.

On the other hand, an evolution has, of course, also taken place within the saprophytic fungi, resulting in a high degree of adaptation to the specific substrates utilized by these organisms. The litter contains a great many secondary plant metabolites, often phenolic in structure, an in some cases, the litter-decomposers have acquired the capability of utilizing such compounds as growth substances. For instance, LINDEBERG *et al.* (1980) found that needle-decomposing basidiomycetes were specifically stimulated by the flavonoid taxifolin glucoside which occurs in pine needles.

HARLEY and SMITH (1983) point out that it is by no means certain that the ability to produce enzymes capable of degrading complex carbon and nitrogen polymers is a general primitive character, as compared with the inability to do so.

Microbial interactions in the mycorrhizosphere are complex. They are characterized by the competition for energy sources and nutrients, resulting in an equilibrium between microbes which, however, changes with time as the plant roots develop. *In vitro* studies on the physiology of different ecological groups of microorganisms, occurring in the mycorrhizosphere, are important for the understanding of the possible functions of these groups. However, at the end of this discussion, some remarks by BOWEN (1979) may be quoted: "The artificial conditions of many experiments, e.g. exudate studies in solution, and spore germination, microbial growth and interactions on agar, have little relation to the behaviour of microorganisms in the rhizosphere. If we are to really understand the kinetics of microbial growth around roots, we have no alternative to studying plants in soil - that is the real world, where we must make our measurements and conduct our experiments."

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